STUDIES ON AUSTRALIAN CAINOZOIC BRACHIOPODS

4. Growth Patterns of the Loop and Cardinalia in Five Recent Terebratellid Species

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ABSTRACT: The developing loops of *Magellania australis* (Quoy and Gaimard), *Neothyris lenticularis* (Deshayes) and *Waltonia inconspicua* (Sowerby) display, during intermedate growth phases, the lacunae considered previously to be characteristic of dallinid development. Lacunae have not been observed in *Pirothyris vercoi* (Blochmann) or in *Jaffaia jaffaensis* (Blochmann), both species possessing an adult loop pattern equivalent to an early intermediate phase of *M. australis*. The solid hinge plates of *N. lenticularis* and *P. vercoi* are preceded in ontogeny by the excavate, lamellar plates characteristic of adult members of *M. australis* and *W. inconspicua*.

INTRODUCTION

Elliott (1953, 1965) in reviewing the loop development of terebratellacean species states that they display two patterns of loop development defined as dallinid and terebratellid. The dallinid pattern is characteristic of the Dallinidae and Laqueidae (now regarded as synonymous with the Kingenidae—see Richardson 1973 b) and the terebratellid pattern is seen in members of the Terebratellidae. The pattern of terebratellid loop development has been assessed from phases observed in five species. In only two of these were the series of described patterns considered to be complete, namely in *Terebratella dorsata* (Gmelin) described by Fischer and Oehlert (1892) and in *Waltonia inconspicua* (Sowerby) described by Thomson (1915). Isolated growth stages only were described by Thomson (1916) for *Jaffaia jaffaensis* (Blochmann), by Douvillé (1879) for *Neothyris lenticularis* (Deshayes) and by Fischer and Oehlert (1892) for *Magellania venosa* (Solander).

The present studies incorporate an account of the developmental patterns of the loop and cardinalia of five terebratellid species. *Magellania australis* (Quoy & Gaimard) is described and figured in detail. Development in the other four species, *Neothyris lenticularis*, *Jaffaia jaffaensis*, *Pirothyris vercoi* (Blochmann) and *Waltonia inconspicua* is described only where it differs from *M. australis*. The development of *W. inconspicua* was re-examined because Thomson (1915) did not include in his series growth phases between 8 mm and 19 mm and because at different sizes but at comparable growth phases *M. australis* showed lacunae in the dorsal bands of the ring.

Shell lengths referred to in the text are always the maximum shell lengths, i.e. the length of the ventral valve. The material figured in this paper is housed in the collection of the National Museum of Victoria (NMV) under the catalogue numbers quoted.

GROWTH STAGES OF THE LOOP AND CARDINALIA

Magellania australis (Quoy & Gaimard)

The development of the loop and the cardinalia is described and figured from a collection of specimens from a depth of 10 m from Westernport Bay, Victoria. The first structure to appear concerned with the formation of the loop is the septal pillar visible as a thickening of the midsection of the dorsal valve at a shell length of approximately 2 mm (Pl. 14, fig. 1). In succeeding growth phases the septal pillar increases in height and extent assuming a roughly quadrilateral lateral outline with the ventral free border or crest of the pillar almost parallel with the dorsal border which is fused with the valve floor (Pl. 14, fig. 2). In this form the septal pillar displays a slight groove in the posterior segment of its ventral crest (Pl. 14, fig. 2, 3, Fig. 1A). The deepening of this groove with the flaring or expansion of the rim produces a small hood or

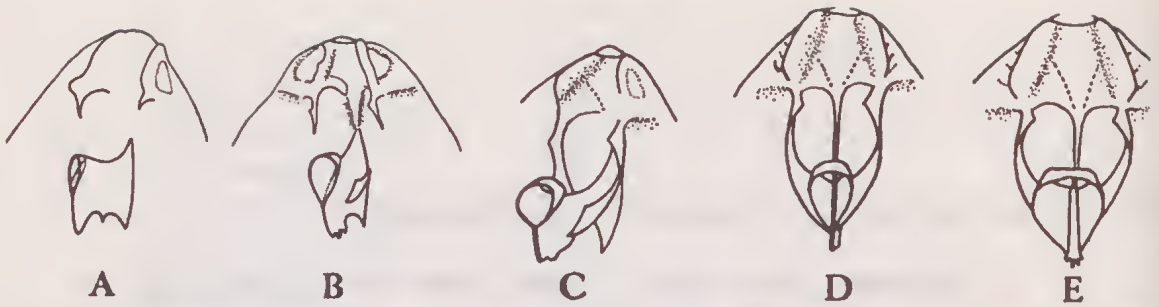* C/- National Museum of Victoria, Russell Street, Melbourne, 3000.

FIG. 1—*Magellania australis*. Line drawings of dorsal valve interiors to illustrate the formation of the ring and the descending branches and, in D and E, variability in the thickness and spinosity of the septum. A, The septal pillar with ventral crest grooved posteriorly. Shell length 2·4 mm, hypotype NMV H193; B, the septal pillar with hood and anterior rudiment of the descending branch of the right hand side. A low median ridge links the pillar with the posterior cardinalia area. The extent to which the hinge plates are excavate posteriorly is indicated by a dotted line. Shell length, 2·4 mm, hypotype NMV H194. C, the median septum (formed from the fusion of the septal pillar with the posterior median ridge) bearing a ring and the anterior attachments of the complete descending branches. Shell length 3·0 mm, hypotype NMV H195. D, shell length 3·1 mm, hypotype NMV H196. E, shell length 3·9 mm, hypotype NMV H197.

cone on the posterior crest of the septal pillar; the septal pillar also carries small triangular plates (anterior rudiments of the descending branches) set obliquely at its approximate mid-height (Pl. 14, fig. 4, Fig. 1B). Resorption of the anterior border of the septal pillar appears to commence at approximately this growth phase, resulting in the jagged or spinous appearance of the anterior border of the pillar in subsequent growth phases. In all these growth phases sockets and socket ridges are defined as are the areas to be occupied by other parts of the cardinalia. A thickening of the posterior margin of the valve marks the area of the future cardinal process and the anterior borders of the developing hinge plates are indicated by thickenings on the valve floor which extend medially from the bases of the socket ridges and the developing crura; a low median ridge extends from this area of the cardinalia to a point just short of the posterior limit of the septal pillar (Fig. 1B).

In the following growth phase (Fig. 1C) the septal pillar is continuous with the posterior median ridge, the two structures combining to form the median septum. These two components of the septum can be differentiated visually in subsequent growth phases, the anterior component being less opaque than the posterior component (Pl. 15, fig. 4 shows the septum in *Pirothyris vercoi*). At this phase the cardinal process is defined and the anterior borders of the hinge plates are separated narrowly from the underlying valve floor, i.e. the hinge plates are anteriorly excavate. The area of the valve floor bounded by the hinge plates, socket ridges and cardinal process is covered by a layer of secondary thickening and thus differentiated from the remaining thin-

ner regions of the valve floor. The descending branches are now complete and resorption of the posterior end of the hood has led to the formation of a ring enveloping the posterior crest of the septum. The oblique lines of attachment of the descending branches to the septum lie parallel with the lines of attachment of the ring.

Variability in the extent, thickness and spinosity of the ventral crest of the septum is apparent in the next two growth phases of comparable maturity (Fig. 1D, E). In these phases the ring envelops most of the crest of the septum, a condition achieved by two processes, the gradual anterior erosion of the septum and the growth of the ring by the accretion of lamellae at its anterior borders. The hinge plates are excavate for about one third to one half of the total length of the cardinal area.

Succeeding growth phases show the gradual anterior convergence of the attachments to the septum of the ring and the descending branches. The anterior fusion of the attachments of the ring and of the descending branches is seen in Fig. 2 A-D. As noted for *Frenulina sanguinolenta* (Gmelin) by Richardson (1973a) this fusion may occur while the septum, partition-like, separates each side of the loop; alternatively the fusion of the attachments may occur simultaneously with the anterior resorption of the septum so that the anterior lines of fusion are free. The hinge plates are excavate for almost the full length of the cardinalia area, the socket ridges forming their lateral boundaries, the medium septum their medial boundaries. At this growth phase crural bases cannot be distinguished from the hinge plates or socket ridges.

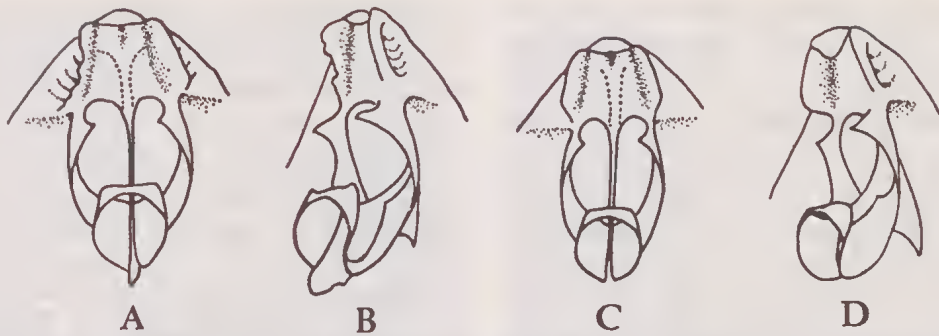From growth phases of approximately 4·3 mm

Fig. 2—*Magellania australis*. Line drawings of dorsal valve interiors illustrating the anterior fusion of the attachments of the ring and the descending branches. Fig. 2A is a ventral view, Fig. 2B a laterally tilted view of the same specimen in which the attachments fuse while the septum extends beyond and separates each side of the loop. Fig. 2C is a ventral view, Fig. 2D a laterally tilted view of a specimen in which anterior resorption of the septum occurs simultaneously with the fusion of the attachments. A-B, shell length 5·0 mm, hypotype NMV H198. C-D, shell length 4·2 mm, hypotype NMV H199.

lacunae may perforate the dorsal segments of the ring (Pl. 14, fig. 5, 6). The lacunae enlarge and breach the posterior borders of the ring, a process which must occur with great rapidity as specimens displaying lacunae are rare compared with those exhibiting the loop phases occurring immediately before or after their appearance (Pl. 14, fig. 7, 8). The adult loop pattern begins to emerge as the result of the concurrent action of the processes referred to previously, i.e. the progressive fusion (in an anterior to posterior direction) of the ring and descending branch attachments, the anterior resorption of the septum, the enlargement of the loop bands by the addition of lamellae on one border with resorption on the other. At a growth phase of 6 mm (Pl. 14, fig. 7, 8) although fragments of the dorsal segments of the ring still adhere to the septum, its anterior borders and ventral segment can now be distinguished respectively as the ascending branches and the transverse band. With the complete resorption of its mid-dorsal and posterior segments no part of the ring remains in contact with the median septum. The attachments of the descending branches to the septum remain in ontogeny to form the lateral connecting bands (Pl 14, fig. 9), the ultimate resorption of which gives the adult loop free of the septum (Pl. 14, fig. 10). This resorption of the bands linking the loop with the septum is correlated with the disappearance of that part (anterior component) of the septum which earlier gave rise to the ring and the descending branches. With the complete fusion of the ring (now translated into transverse band and ascending branches) and the descending branches, only the posterior component appears to represent the adult septum.

In adult specimens of *M. australis* he examined, Allan (1939) described the presence of crural

bases which were fused with the socket ridges. In many specimens examined by the author there is no identifiable structure lying between the socket ridges and the hinge plates; in some specimens ridges, in others linear depressions, form traces of the crura in these areas.

Neothyris lenticularis (Deshayes)

The only description of the developing loop of *N. lenticularis* is that of Douvillé (1879) who illustrated two growth phases from an unnamed locality. These figures show the loop after the fusion of the ring and the descending branches and with an elevated septum lying between the fused attachments.

These studies show that the same growth patterns of the loop follow the same sequence in *N. lenticularis* (trawled at 80 m off Oamaru, New Zealand) as they do in *Magellania australis*. In addition, despite the larger average adult size of *N. lenticularis* (48 mm as compared with 32 mm for *M. australis*) the different developmental patterns occur at the same approximate shell size as they do in *M. australis*. In both species at a ventral valve length of approximately 2·5 mm a ring and incomplete descending branches are present, at 3·0-3·5 mm the descending branches are complete, at 4·0-5·5 mm the attachments of the ring and the descending branches fuse anteriorly and lacunae appear in the dorsal segments of the ring, at 6·0 mm the penultimate loop phase is evident with lateral connecting bands only linking the loop with the septum.

The development of the cardinalia also shows a similar pattern to that described for *M. australis*. However the two species differ in the earlier definition and development in *N. lenticularis* of the hinge plates, the cardinal process,

and the posterior median ridge which also combines at a relatively earlier stage with the septal pillar to form the median septum. At a growth phase of 5 mm these parts of the cardinalia are thicker than the equivalent structures in adult specimens of *M. australis*. Crural bases are not differentiated as structures distinct from either the socket ridges or the crural bases at any growth phase. The hinge plates, like those of *M. australis,* develop as excavate structures (Pl. 14, fig. 11, 12) but in later growth phases, as a result of secondary thickening, they fuse with the valve floor. There is a general deposition of secondary thickening in the posterior region of the valve so that, in addition to the hinge plates, the socket ridges, cardinal process and septum all become thick and heavy. In the young adult illustrated in Pl. 14, fig. 12, the thickening is sufficient to alter the outline and extent of the socket ridges and cardinal process but the hinge plates remain excavate anteriorly. Adult specimens of *N. lenticularis* in which the hinge plates are thick and completely fused with the valve floor are described and illustrated in Neall's recent review (1972) of the genus *Neothyris*.

Waltonia inconspicua (Sowerby)

The development of *Waltonia inconspicua* has been examined in examples of the species from two New Zealand inter-tidal localities, Purau Bay in Lyttleton Harbour and Chatham Islands. The patterns seen in the series from Purau Bay correspond well with that described for *Magellania australis* and they occur within a comparable size range. Although they achieve a similar average adult size, i.e. a length of 20-24 mm, the specimens from Chatham Islands examined are characterized by the relatively later inception of intermediate loop patterns, e.g. lacunae appear at a growth phase of approximately 12 mm instead of at the 4-6 mm phases of *W. inconspicua*. The development of the cardinalia also corresponds with that described for *M. australis* and crural bases were not apparent in any of the specimens examined.

In 1915 Thomson described the loop development of examples of *Terebratella rubicunda* = *Waltonia inconspicua* from three New Zealand localities: Cook Strait, Foveaux Strait and Wellington harbour. Thomson noted that the development of *W. inconspicua* differed in no important respect from that of *Magasella sanguinea* (Leach) examined by him (loc. cit.) and of *Terebratella dorsata* (Gmelin) described in 1892 by Fischer and Oehlert. Thomson does not describe any growth phases of *W. inconspicua* between 8 mm (= magelliform phase) and 19 mm (= terebratel-liform phase) but it is strange that neither he nor Fischer and Oehlert observed the presence of lacunae in any of these species, while they are found to be present in specimens of *W. inconspicua* examined by the author (Pl. 15, fig. 8). The first appearance of the lacunae in the band forming the ring is followed rapidly by their enlargement to breach the posterior borders of the ring so that specimens displaying lacunae are rare. However, it is not uncommon to find evidence of their earlier existence in the shape of the band forming the ring. Therefore it is possible that in some species or even populations of the same species the early ring may be formed by a band of narrower diameter than is the case in the series examined here. All parts of the loop grow by the simultaneous accretion of lamellae on one edge and resorption at the other. Such a gradual and continuous process may be sufficient to reduce the diameter of the band of a narrow ring, consequently the presence of lacunae indicating the need for more extensive resorption would not be required. Therefore it is concluded that there may be a direct relationship between size and the method by which parts of the ring are resorbed. This supposition implies that two methods of resorption of the ring may exist in the one species if there is variation in the width of the band forming the ring. In *W. inconspicua* such variation does not seem unlikely for Thomson notes 'there is a great deal of latitude in the relations between size of shells and stage of loop-development attained' (1915, p. 406). Thomson does not relate differing sizes with the three localities from which he obtained specimens. However, as noted above, there seem to be differences in the shell size of the same developmental pattern found in specimens of *W. inconspicua* from Purau Bay and from the Chatham Islands. How consistent these differences are and whether there is also variation in the size of the ring and the pattern of its resorption can be determined only by the study of greater numbers of specimens from the many different localities in New Zealand in which *W. inconspicua* is present.

Pirothyris vercoi (Blochmann)

The development of *P. vercoi* agrees with that of *M. australis* in the sequence of early loop patterns present. It differs from *M. australis* in the smaller shell size at which these patterns occur and in the earlier definition of the elements of the cardinalia. These differences are probably associated with the smaller adult size of *P. vercoi* (average length 7 mm) compared with that of *M. australis* (32 mm). The adult loop pattern of *P. vercoi* is comparable with that of *M. australis*

before the appearance of lacunae in the band forming the ring in the latter species, i.e. when the ring and descending branches are fused anteriorly but posteriorly are separately attached to the septum.

At a shell length of 1·8 mm (Pl. 15, fig. 1) the dorsal valve displays a low septal pillar which, at a growth phase of 2·8 mm (Pl. 15, fig. 2), develops into a high, blade-like structure bearing a hood on its posterior border and descending branch rudiments on its lateral surfaces. In both growth phases the elements of the cardinalia are well defined and lamellar hinge plates are anteriorly excavate for about half the distance between their anterior borders and the cardinal process. In the 1·8 mm growth phase a low median ridge extends from the cardinalia to a point near the posterior limit of the septal pillar and at 2·8 mm these two structures are continuous forming the median septum. As a result of the resorption of its posterior end the hood becomes a ring and at a growth phase of 3·3 mm (Pl. 15, fig. 3) the descending branches are complete. Between shell lengths of 3-4 mm the posterior surface of the cardinal process begins to assume its characteristic adult trefoil shape and the hinge plates and other parts of the cardinalia thicken. The posterior regions of the valve and the cardinalia thicken rapidly so that in growth phases of more than 4 mm the hinge plates are no longer excavate but are fused with the valve floor. Further development of the loop is not necessarily related to size so that specimens with a length greater than 4 mm can display two different loop patterns. One pattern is an enlarged version of the previous growth phase with the ring (now occupying the entire length of the crest of the septum) and descending branches attached separately to the septum (Pl. 15, figs. 5, 6). In the second and more advanced pattern there is anterior fusion of the descending branch and ring attachments but posteriorly they remain separately attached to the septum (Pl. 15, fig. 7).

The appearance and development of the septum are noteworthy in *P. vercoi*. The septal pillar bearing the early hood is, in relation to dorsal valve size, higher and narrower in lateral outline than it is in the other terebratellid species described in this paper. There seems to be little or no erosion of its anterior border, a process which commences almost as soon as the pillar is formed in other species. The septal pillar unites with the posterior median ridge to form the median septum early in development (2·8 mm herein). Further growth of the septum appears to occur predominantly in that region derived from the median ridge (posterior component) so that this enlarged

component replaces the attachment of the septal pillar to the valve floor. In other words the anterior component of the septum (the septal pillar bearing the ring and the anterior attachments of the descending branches) appears to sit on top of that portion of the septum derived from the posterior median ridge. As noted in the previous description of the developing septum of *M. australis,* visual differences are apparent in the septal components. In the photograph (Pl. 15, fig. 4) an attempt is made to illustrate these differences in *P. vercoi.* The anterior segment of the septum bearing the parts of the loop is more translucent than the remainder of the septum. The low posterior segment of the septum linking the pillar with the cardinalia is more opaque and, as noted above, appears gradually to engulf or replace that portion of the anterior segment lying below the descending branch attachments.

Jaffaia jaffaensis (Blochmann)

Thomson (1916) examined several early loop phases of *J. jaffaensis* and from these concluded that, while there were resemblances to the loop of *Campages* (Dallinidae) the genus *Jaffaia* should be referred to the Magellaniinae (= Terebratellidae). This reference to the Magellaniinae was based upon the absence of dental plates and on the separate attachment to the septum of the descending branches and the loop in early growth phases of *J. jaffaensis.* In 1927 Thomson transferred the genus, with reservations because of the absence of dental plates, to the Dallininae (= Dallinidae) stating that while the separate attachment of the descending branches and ring did not occur in *Dallina* and *Macandrevia* it had been described in *Dallinella* by Beecher (1895). Allan (1940) shifted *Jaffaia* back to the Terebratellidae claiming that other dallinid genera without dental plates, viz. *Campages* and *Dallina* display a septum passing under excavate hinge plates. In the possession of a hinge trough associated with a bifurcating septum Allan stated that *Jaffaia* was more appropriately placed in the terebratellid subfamily, the Neothyrinae. The appearance of an apparently bifurcating septum results from the thickening of the septum and the hinge plates. In *J. jaffaensis,* as in the other species described herein, the hinge plates develop as excavate structures which fuse on top of the median septum. The hinge plates extend forward medially and anteriorly onto the crest of the septum so that their anterior border is V-shaped. In later growth phases they, together with the septum, thicken but remain excavate anteriorly.

The early phases of loop development of *J. jaffaensis* are similar to those already described

for *M. australis* and for *N. lenticularis*. At a
growth phase of 1·8 mm a high septal pillar
arises from the mid-line of the dorsal valve, and
at 2·4 mm the pillar bears descending branch
rudiments and a hood. Following this early growth
phase, differences between *M. australis* and *J.
jaffaensis* are apparent in the form and extent
of the ring. The development of the ring from
the hood in *J. jaffaensis* is accompanied by rapid
growth along the anterior to posterior axis of the
attachments of the ring to the septum so that at
a growth phase of 4·0 mm these dorsal segments
are approximately ten times as wide as the ventral
segments of the ring (Pl. 15, figs. 9, 10). This
differential growth of the band forming the ring
results apparently in the cross section of the ring
changing from a circular outline to one of an
incomplete circle topped by an inverted V. As
development proceeds the differences in width of
the parts of the band forming the ring become
less pronounced, consequently at a growth phase
of 8 mm a cross section of the ring is again
subcircular (Pl. 15, figs. 11, 12). At this phase
also there is anterior fusion of the attachments
of the descending branches and the ring. In the
adult loop of *J. jaffaensis* (Pl. 15, fig. 13) these
attachments are fused for approximately three
quarters of their length and posteriorly they are
attached separately to the septum.

At present *Jaffaia* is retained in the Terebratel-
lidae. However, since the genus displays features
shared by some members of both the Dallinidae
and the Terebratellidae, its systematic position
remains uncertain. It is discussed in relationship
to these families in a subsequent paper in which
the family Dallinidae is redefined.

DISCUSSION

Major steps in the formation of the terebratellid
loop are:
1. The formation of axial structures, a septal
pillar bearing a ring (preceded by a hood) and
descending branch rudiments.
2. The fusion of these structures with posterior
components from the cardinalia region to form
descending branches and a median septum.
3. The growth and fusion of the ring and
descending branches, a process culminating in a
loop free of the septum but attached posteriorly
to extensions of the cardinalia, the crura.

The formation of the ring and the descending
branches is followed by their anterior fusion and
separation from the septum while posteriorly each
structure remains attached separately to the
septum. This growth pattern is seen as the adult
loop of *J. jaffaensis* and *P. vercoi* which differ

in the width of the bands forming the ring and
the descending branches. In the other species
described this phase is succeeded by extensive
resorption of segments of the ring so that its
posterior attachments to the septum are lost.
Thus only the descending branch attachments
remain on the septum as the lateral connecting
bands. This pattern is the adult loop form of
W. inconspicua and the resorption of the con-
necting bands results in the adult loop seen in
M. australis and *N. lenticularis*.

In *W. inconspicua*, *M. australis* and *N. lenti-
cularis* lacunae are described in those segments
of the ring which are resorbed after the anterior
fusion of the ring and descending branch attach-
ments. Lacunae are regarded as characteristic of
dallinid loop development but have not been
described previously in the development of any
terebratellid species. The brachiopod loop de-
velops by 'the accretion of lamellae on one edge
and simultaneous resorption on the other' (Rud-
wick 1970, p. 128). The presence of lacunae
probably indicates the need to establish more
extensive lines of resorption, a need associated
with a greater degree of early calcification. There
could be two reasons why lacunae have not been
noted previously in the developing loops of the
three terebratellid species described in this study.
In the first place the presence of complete lacunae
is rare as a result of their rapid enlargement to
breach the posterior borders of the ring. Over
100 specimens of *M. australis* were examined
before finding a ring with the identity of the
lacunae still intact. Secondly, it is possible that
the presence of lacunae is a variable character in
some terebratellid genera or even species. Their
presence is associated apparently with a band of
greater width than that which can be resorbed by
the gradual erosion of its posterior borders. In any
species in which the band forming the ring varies
sufficiently in width it is possible that more than
one line of resorption is required to produce loop
bands of adult dimension. As indicated on p. 200
such variation may be found in different popula-
tions of *W. inconspicua*.

Cooper (1973) recently described the loop
development of *Magellania venosa* (Solander)
and of his new species *Aneboconcha obscura*.
In neither species does he describe the presence
of lacunae at any growth phase. Cooper's photo-
graphs of *M. venosa* show that it possesses a ring
composed of a relatively narrow band and in
which there is no evidence of the existence of
lacunae. On the other hand *A. obscura* possesses
a wide ring band and two photographs of the
developing loop of this species (Cooper 1973,
Pl. 4, figs. 9, 10) show a ring pattern similar to

that of *M. australis* at a comparable phase (illustrated Pl. 14, figs. 7, 8), i.e. in which the shape of the band forming the ring gives evidence of the earlier presence of lacunae.

Other variables noted in this study are the extent, thickness and degree of spinosity of the septum and the extent of anterior septal resorption relative to the fusion of ring and descending branch attachments. All these features show as much variation within one species as they do between different species. In one species, *Pirothyris vercoi*, there is little variation in septal shape and little or no spinosity although the adult loop varies in the extent of its attachment to the septum. There is general conformity in the shell size at which different growth patterns of the loop occur in *M. australis, N. lenticularis* and *J. jaffaensis* despite large differences in average adult size. On the other hand *W. inconspicua* shows much variation between different populations and in *P. vercoi,* the smallest adult species, early loop patterns occur in shells of smaller size than they do in the other species.

In these Recent terebratellid species the median septum, as described by Baker (1972) for the Jurassic species *Zeilleria leckenbyi*, is the result of the fusion of two components, the anterior septal pillar and a posterior median ridge. The pillar appears first in ontogeny and resorption is apparent in its anterior border at about the time it is united posteriorly with the median ridge. Further development entails the gradual replacement by the posterior component of the anterior component which is resorbed and finally disappears with the loss of its last links with the loop, the lateral connecting bands. These steps can be traced because the two components of the septum are composed of shell matter differing visually in density (Pl. 15, fig. 4). The septum, like the bands of the loop, is a structure developing by growth on one border and resorption on the other, the loop growing by the accretion of lamellae, the septum by the deposition of thickening. Whether or not these structures differ only in thickness is not clear, as the structure of the shell has not been part of this study. Williams (1968) states that the predominantly impunctuate septum of *Laqueus* contains a punctuate strip of shell, the position of which does not appear to coincide with the boundaries of the different septal components noted in this study. This difference in shell density is seen also at the areas of union of the descending branches and the crura (Pl. 14, fig. 12), i.e. the crura and the anterior septal component are more translucent than the bands of the loop and the posterior septal component.

The development of the cardinalia is similar in all the species studied. The socket ridges are the first structures to appear and the cardinal process is forecast early in development as the thickened posterior margin of the valve. Other structures, the hinge plates and the crura, appear to emanate from the anterior bases of the socket ridges. Crural bases, visible as ridges lying between the socket ridges and the hinge plates, are apparent only in the late development phases of some specimens of one species, *M. australis.* The relationship of the hinge plates to the septum is noteworthy. The term 'hinge plate' has been applied in the past only to excavate plates occupying the area between the socket ridges and serving for the attachment of the dorsal pedicle muscles. During development in the species described here the hinge plates fuse medially on the crest of the septum so that they form an excavate platform buttressed medially by a median septum. The hinge plates extend forwards anteriorly and medially onto the septum so that their anterior border is V-shaped in outline. If secondary thickening occurs the septum, as a result of its position at the point of the V of the border of the thickened hinge plates, gives a superficial appearance of bifurcation. A hinge trough is defined in the Treatise (1965) as a structure 'formed by the fusion of a bifurcated median septum with combined socket ridges and crural bases of some terebratellaceans' (Elliott H146). The terebratellaceans alleged to display a hinge trough include *Neothyris, Jaffaia* and *Pirothyris* which are shown in this study to possess solid or thickened hinge plates preceded in ontogeny by excavate structures.

The significance of the apparent bifurcation of the septum, the presence of crural bases and of excavate hinge plates, factors used previously in the differentiation of subfamilies, will be discussed in a future paper on Australian terebratellid brachiopods.

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EXPLANATION OF PLATES 14-15

PLATE 14

Magellania australis (Quoy & Gaimard)
(10 m Westernport Bay, Victoria)

FIG. 1-4—Stereoscan photomicrographs of the dorsal valve interiors of three specimens each with a shell length of approximately 2·0 mm and showing: 1. The early septal pillar, × 67, hypotype NMV H190. 2. The septal pillar (before resorption commences) and parts of the cardinalia, the socket ridges (ridge on left-hand side broken), crura and developing hinge plates, × 33, hypotype NMV H191. 3. An enlargement of the septal pillar in fig. 2 which shows the slight groove (which precedes hood formation) apparent in the most posterior segment of the ventral crest of the pillar, × 100. 4. The septal pillar with the hood enveloping its posterior crest and rudiments of the descending branches extending from its lateral surfaces, × 100, hypotype NMV H192.

FIG. 5, 6—Two dorsal valve interiors showing the lacunae which perforate the dorsal band of the ring. In both specimens the right-hand side of the ring is broken. 5. Shell length 5·75 mm, hypotype NMV H200. 6. Shell length 5·0 mm, hypotype NMV H201.

FIG. 7, 8—Ventral and lateral views of the loop of a specimen in which the posterior walls of the ring have been breached by the enlargement of lacunae. Evidence of the earlier presence of lacunae is indicated in the shape of the band forming the ring and which now forms the ascending branches and the transverse band. Shell length 6·0 mm, hypotype NMV H202.

FIG. 9—Penultimate loop pattern in which the descending branches only remain attached to the septum, these attachments now being referred to as the lateral connecting bands. Shell length 8 mm, hypotype NMV H203.

FIG. 10—Adult loop pattern. Shell length 19 mm, hypotype NMV H204.

Neothyris lenticularis (Deshayes)
(80 m off Oamaru, New Zealand)

FIG. 11—A young specimen displaying lamellar hinge plates. At this growth phase the ring and the descending branches are separately attached to the septum; part of the ring on the left-hand side is broken in this specimen. Shell length 5·1 mm, hypotype NMV H206.

FIG. 12—Young adult specimen with thick but anteriorly excavate hinge plates. Note the thickening of all parts of the cardinalia and the difference in shell density apparent at the line of union of the descending branch and the crus on the left-hand side. Shell length 38 mm, hypotype NMV H207.

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PLATE 15

Pirothyris vercoi (Blochmann)
(40 m Backstairs Passage, South Australia)

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FIG. 1—Dorsal valve interior with septal pillar. Shell length 1·8 mm, hypotype NMV H209.

FIG. 2—The septal pillar with a ring on its posterior crest and a descending branch attachment barely visible on its lateral surface. Posterior descending branch rudiments extend from the cardinalia. Shell length 2·8 mm hypotype. NMV H210.

FIG. 3—Growth phase in which the descending branches are complete, their attachments to the septum (formed by the fusion of the septal pillar with a posterior component) lying underneath those of the ring. Hinge plates are excavate at this growth phase. Shell length 3·3 mm, hypotype NMV H211.

FIG. 4—Lateral view of the median septum of a specimen of a young adult to illustrate the visual differences in density in parts of the septum (anterior border of the septum to the left of the photograph). Both the ring and the descending branches have been removed, the descending branch attachment to the septum is visible as an oblique line on its lateral face, the ring attachment as a line/ridge just below the crest of the septum with which it is almost parallel. The low posterior segment of the septum linking the anterior pillar with the cardinalia is apparent as a structure of greater opacity than the remainder of the septum. Shell length 5 mm hypotype NMV H214.

FIG. 5, 6—Ventral and laterally tilted views of a specimen 5·5 mm in shell length, hypotype NMV H212.

FIG. 7—Ventral view of a specimen 5·0 mm in length, hypotype NMV H213.

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Waltonia inconspicua (Sowerby)
(Purau Bay, Lyttleton Harbour, New Zealand)

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FIG. 8—Dorsal valve interior with juvenile loop showing lacunae in the dorsal segments of the band forming the ring. The descending branches are obscured by the dried soft parts adhering to the skeleton. Shell length 6·0 mm, hypotype NMV H208.

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Jaffaia jaffaensis (Blochmann)
(300 m off Cape Jaffa, South Australia)

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FIG. 9, 10—Ventral and laterally tilted views of the early loop with the ring and the descending branches separately attached to the septum and the ring displaying its anterior V-shaped extension. This specimen (length 4·0 mm, hypotype NMV H215) coated with magnesium oxide.

FIG. 11, 12—Ventral and laterally tilted views of a loop displaying anterior fusion of the ring and descending branch attachments. Shell length 8·0 mm, hypotype NMV H216.

FIG. 13—Loop of an adult specimen coated with magnesium oxide. Shell length 16·0 mm, hypotype NMV H217.